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Neuroptera and Biological Control (Neuropterida)

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Abstract

Abstract: Members of three families of Neuroptera (Coniopterygidae, Hemerobiidae, Chrysopidae) have been used in biological and integrated control, mainly of field crop pests, and in augmentation programmes to increase the impacts of natural enemies. Most emphasis has been in use of a limited range of Chrysopidae, predominantly *Chrysoperla* spp. These developments are outlined and discussed to provide a broad perspective of current uses of lacewings in integrated pest management and how uses might expand in the future.

Key words: lacewings, snakeflies, Chrysopidae, Hemerobiidae, Coniopterygidaepest management, predators, pesticides.

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Introduction

Most neuropteroid insects are predators, both as larvae and adults. Although other feeding habits occur in the lacewings, the above uncritical generalisation has led to considerable interest in using terrestrial lacewings as biological control agents able to devour pest insects and reduce their populations on a wide variety of field, orchard and glasshouse crops. They thus vie with Coccinellidae and other groups of predatory insects as popular biological control agents in many parts of the world. Considerable research has been undertaken to determine and quantify their influences, and how they may be manipulated for enhanced impacts on pest populations. As with many other insect groups, such 'applied relevance' has been the major stimulus to research and the single most important factor leading to increased biological understanding of neuropteroids, and of the subtle but far-reaching biological differences between closely related taxa.

Many different neuropteroid groups have been implicated as important predators in various ecosystems, because of their abundance, and their seemingly close and consistent associations with particular habitats and/or prey taxa, coupled with their voracity and high fecundity. However, in practice members of only three families of Neuroptera have proved more broadly amenable to such assessment and employable in pest management programmes. Indeed, the lacewings currently of interest as biological control agents comprise only limited spectra of 3 of the 17 recent families of Neuroptera, namely Coniopterygidae, Hemerobiidae and Chrysopidae, with by far the greatest attention given to the last-named, the green lacewings (NEW 1975, CANARD et al. 1984, MCEWEN et al. 1999). In consequence, we know far more of the biology of these taxa than of most other Neuroptera.

Neuroptera are not one of the more diverse groups of predators in most agricultural systems, and can be far outnumbered by groups such as Araneae, Carabidae, Staphylinidae, Coccinellidae, Syrphidae and some Heteroptera as generalist predators. Thus, in an extensive survey of arable land in Switzerland, DUELLI & OBRIST (1995) collected 599 predatory species of the above groups: only 23 were Neuroptera, and these totalled 743 individuals of the overall nearly 124000 predators collected. More broadly, SUNDERLAND et al. (1996) cited predator richness of around 400 generalist species in cereals in Britain, and of 600-1000 species in cotton and soybean crops in the United States. Nevertheless, Neuroptera remain one of the few groups which, in practical IPM terms, may be considered 'aphidophagous'. They have thus attracted attention for use against a wide variety of small prey arthropods, in a great variety of agricultural, orchard and forestry crops.

This account is a broad survey and evaluation of the use of lacewings in biological control, with some discussion of future directions and their incorporation into increasingly effective integrated pest management programmes. The main topics reviewed are:

1. The taxa of lacewings useful in biological control.

2. The rationale, principles and practice of biological control.

3. The place of lacewings in integrated pest management.

4. The production and manipulation of lacewings for pest management.

Why these taxa?

Early records of lacewings as predators emphasised the voracity and behaviour of larvae, in particular. The conical pits formed by certain myrmeleontoid larvae, in which they lie buried except for the jaws exposed awaiting the arrival of insects such as wandering ants which they subdue by dragging under the substrate, are known widely as one of the classic examples of insect predators. Likewise, chrysopid larvae camouflaged by the debris from past captures are evocative as 'aphis-lions', paralleling the 'antlions' above. Such examples led to broad assumption that most lacewings could be valuable as predators in crop protection, but this has not been substantiated. Thus, antlions and their relatives tend to occur in relatively natural habitats, often not associated with vegetation or with the insects that feed on it. Despite their considerable abundance and diversity in areas such as the more arid

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regions of southern Africa (leading MANSELL & ASPÖCK, 1990, to comment on their importance as significant predators) and Australia, such areas are usually not those used for intensive crop production. The long life cycles of many such taxa render them somewhat nonresponsive to rapid changes in prey spectrum and density. As importantly, though, many are 'ambush predators' which do not actively search for prey but await it coming to them.

In contrast, many members of Coniopterygidae, Hemerobiidae and Chrysopidae are associated primarily with vegetation (sometimes of restricted subsets, such as coniferous or broadleaved trees, or trees versus low vegetation: MONSERRAT & MARIN 1996) and feed almost exclusively on small herbivorous arthropods representing groups which also contain pest taxa, and for which they actively search. Lacewing larvae can move considerable distances to seek prey. Unfed hatchling larvae of *Conwentzia pineticola* can travel more than 40m and survive for more than 10 hours before feeding, for example (FLESCHNER 1950). Likewise, newly hatched chrysopid larvae can survive for up to 72h without food, or up to 9d if given water (SUNDBY 1966), and may search actively for prey over most of this time. As such, they are to some extent 'preadapted' for manipulative use in similar environments and to exploit related prey. Most of the species of interest frequent the temperate zones with strongly seasonal climates, those regions used most intensively for diverse, intensive agriculture. They tend to have well-defined patterns of voltinism, with one to several generations a year, and can respond numerically to increased prey density within a season. All can at times be abundant in their natural habitats, and may show well defined peaks of abundance, conferring synchronicity with predominant prey species. Within a habitat a sequence of different lacewing species can peak at different times of the growing season for considerable collective effect on longlived pests or those present for extended periods.

Sporadic advocacy for use of other neuropteroids in biological control, such as for Psychopsidae (TILLYARD 1919) and Raphidioptera, has not led to any constructive adoption and, in general, most other groups are not likely to be utilised in the foreseeable future. As ASPÖCK et al. (1991, see also H. ASPÖCK 1991) noted, further investigation of the predatory role of Raphidioptera is needed, because their large numbers in some environments suggest that they could be significant. Recent surveys in Italian vineyards (PANTALEONI 1990, LETARDI 1994) showed the snakefly *Parainocellia bicolor* (COSTA) to be abundant, and it may have some value as a predator on such longlived plants. However, simple numbers do not prove a regulatory role for predators on prey, and there is no quantitative evidence for values of Raphidioptera as biological control agents. Although larvae of some Berothidae feed on termites (JOHNSON & HAGEN 1981), their general scarcity renders their likely use in control insignificant. However, although there is no quantitative evidence to support the suggestion, it is possible that local high densities of Myrmeleontidae could be inimicable with biological control programmes through devouring beneficial predatory ants.

Taxonomic introduction to the families involved

Coniopterygidae, dusty-wings, are an isolated lineage of Neuroptera and are the smallest members of the Neuroptera. Most species have forewings only 2-3 mm long, and they are recognised by the reduced venation and the wings and body covered by white or greyish wax. The global fauna was monographed by MEINANDER (1972), who later (MEINANDER 1990) provided an augmented checklist of world species. Coniopterygidae are widespread but, as for the other families treated here, many of the genera and species have more restricted distributions. Hemerobiidae, brown lacewings, and Chrysopidae, green lacewings, are also widespread. These two families have traditionally been treated as closely related, but U. ASPÖCK (1992) has noted that this supposed alliance may be based on inadequate appraisal of characters.

Recent taxonomic surveys have done much to clarify the integrity and relationships of the genera in each family. OSWALD (1993) reviewed the genera of Hemerobiidae, and BROOKS & BARNARD (1990) elucidated the

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features and relationships of the mass of chrysopid genera earlier masquerading under the name '*Chrysopa*', and defined the limits of this genus effectively for the first time. Most earlier literature on Chrysopidae includes generic combinations incompatible with these modern definitions, and care is needed in its interpretation, even in relatively well known faunas.

Higher groupings, subfamilies, of the three families are generally clearly definable, though the relationships between some of them are unclear. Many structural characters are used for definition at subfamily and genus levels, and include many features of wing venation and body. Genitalic arrangement can be of critical importance, and many female chrysopids can still be placed only tentatively to genus if unaccompanied by the more distinctive males. Genitalic features are of almost universal importance for separating species.

The three families are all diverse; Coniopterygidae comprises around 450 described species, Hemerobiidae about 550 species, and Chrysopidae contains around 1200 described species. The genera of current interest in biological control were reviewed by NEW (1999). Briefly, these include 7 genera of Coniopterygidae, 5 of Hemerobiidae and about 12 of Chrysopidae, but those included simply reflect historical opportunism and implication (often based on only a single species in a genus) rather than the outcome of more comprehensive surveys of the total utility of each family. Thus, whereas both main subfamilies of Coniopterygidae are represented, all Chrysopidae included belong to one tribe (Chrysopini) of the largest subfamily (Chrysopinae). Most of the taxa implicated represent large genera or those represented in northern temperate regions where interest in biological control was initiated and where their incidence in association with putative pest taxa on crops has been more thoroughly documented. The almost total lack of knowledge of the biology of most tropical lacewings implies strongly that other suitable candidates could be revealed in due course. However, some taxa appear not to have potential applied value. Species of the large chrysopid genus *Italochrysa* PRINCIPI, for example, apparently feed as larvae on ant brood as inquilines, so that the spectrum of potential biological control agents is probably rather more limited than popularly supposed, and becomes more so if we exclude the numerous rare and ecologically specialised taxa whose use would necessitate excessive manipulation of their normal biology - in as far as this can be predicted. However, other commentators take a broader view, that the potential for lacewings in biological control has scarcely been tapped, and that many more taxa will eventually be found useful.

Within the range of taxa noted above, the vast majority of attention has devolved on one small group of chrysopids, sometimes referred to simply as '<u>the</u> green lacewing', namely the sibling species of the *Chrysoperla carnea* (STEPHENS) group. Because of the taxonomic and biological confusion which has persisted within this group, it is noted separately here, to alert readers to the inherent complexities which can occur in many groups of natural enemies and hinder clear interpretation of their use in pest management.

The *Chrysoperla carnea* problem

The taxonomic and other interpretative challenges of this complex of presumed sibling taxa are by no means solved. The precise number of taxa included in the complex is still unclear. "C. *carnea*" was long considered to be polymorphic and variable in northern temperate regions, and complex series of names have been applied both in Europe and North America to account for this variability. Examination of a wide range of characters, such as courtship songs, adult and larval morphology, enzyme polymorphisms, variation in diapause regime and other ecophysiological features have confirmed the presence of at least six members of the group in Europe alone (THIERRY et al. 1998). Many areas have at least two sympatric species (DUELLI 1996), and the notion of different taxa occurring together is now replacing the concept of a single, variable entity (THIERRY & ADAMS 1992).

The taxonomic details of this complex are relevant here only in relation to the inadvertent confusions that have occurred in the past, and their wider relevance to confusion between exotic and native biological control agents. In retrospect, early attempts at intro-

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duction such as the release of putative C. *carnea* from the Indian subcontinent into North America to control spotted alfalfa aphid in the 1950s (ADAMS in THIERRY & ADAMS 1992) are impossible to analyse, as the released species was not differentiated from the very similar C. *plorabunda* (the 'lead species' of the complex in North America). Such differentiation, indeed, might not then have been possible. Of greater concern is the current practice in Europe of distributing insectary stocks widely across international boundaries. Thus, insectary stocks from northern Italy have frequently been exported for release in countries in more northern parts of Europe under the guise of C. *carnea*. Some of those releases are undoubtedly of species alien to the new areas, undetected because of lack of critical appraisal of the various taxa possibly present. It is doubtful whether the nature of some such introductions can ever be clarified but, in order to avoid further confusion, careful documentation of the origin of biocontrol stocks purported to be of the same species is needed, together with responsible deposition of voucher specimens for future reference.

Biological control

Widespread global concern over the use of pesticides, ranging from problems of pest resistance to side-effects on non-target organisms and dissemination and accumulation in the wider environment, during the last few decades have stimulated development of increasingly sophisticated management strategies against a wide variety of agricultural, orchard and other arthropod pests. A predominant component of such integrated pest management programmes is the use of parasitoids, predators and pathogens affecting the pest, collectively its 'natural enemies'. Two major contexts have been pursued, both diverse, but which are very different in their ecological implications:

1. "Classical biological control" involves the importation and release of natural enemies from a pest's native range to attack it in areas where it is exotic. Pest status often arises in part because of release from the factors which limit population numbers in a natural, balanced context. Thus in Australia many of the major agricultural and environmental weeds are exotic species and use of specific herbivores from their areas of origin is a key component of control. Likewise, many insect pests (such as the majority of aphid species in Australia) are exotic species, colonising only after their host plants had entered cultivation, and use of imported natural enemies is a focus for integrated control.

2. Some natural enemies, particularly predators, are likely to be already present in the areas where a pest occurs. It may be possible to foster, intensify and augment their effects on the pest population, thereby using native species rather than imported control agents. These native taxa can then be reared in captivity in large numbers for augmentative release, usually on a periodic basis to match the characteristics of annual cropping systems. This approach can avoid the problems of introducing yet further exotic species into possibly sensitive environments, and use of native species of predators is widely forecast to increase in the future (WAAGE 1992). PARRELLA et al. (1992) also noted the current and future values of this strategy.

The two approaches are not necessarily mutually exclusive, in that once an exotic species becomes established and naturalised as part of the regular fauna it can be manipulated in similar ways to a native species.

Massive benefits have occurred from both approaches in the past, and are likely to continue as biological control is increasingly a key component of many pest management strategies. However, the practice of classical biological control has also engendered considerable concerns and debate in recent years, over the safety of the agents used. Introduction of any exotic species (that is, one new to the site of introduction) imposes a duty of care for the receiving environment. This normally involves assurance of specificity - so that an introduced herbivore will not stray from its target weed to eat native or other desirable plant species, or an introduced predator also attack sensitive native taxa. Debate has accelerated following HOWARTH's (1983, 1991) implication (albeit without quantitative scientific evidence) that large numbers of endemic Hawaiian insects may have become extinct due to introduced parasitoids and predators which

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have spread from crops into natural ecosystems on these remote islands. NAFUS (1994) implied a similar situation for Guam, and such appraisals have led to much wider debate over the environmental safety of classical biological control agents. The broader credibility of classical biological control has suffered accordingly, and many authors (such as SAMWAYS 1988, 1994; SANDS 1997) have stressed the need for balanced appraisal of 'acceptable risk'; as SANDS noted "The success and environmental benefits from introduction of narrowly specific exotic agents are often overlooked with more public attention given to the impact by generalist predators on native species".

There is an important dichotomy in the practice of classical biological control as used against plant weeds and arthropod pests. Screening of herbivores introduced against weeds is well-established, with sound protocols which do much to guarantee the specificity, hence the environmental safety, of the agents. Simplistically, any tendency for the herbivore to eat other unrelated plant taxa is likely to lead to its rejection from further consideration. Plants of conservation concern may be incorporated routinely into the spectrum tested. In contrast, screening of predators against pest arthropods is much less advanced and, until recently, has often been very superficial or generalised; basic protocols are still being developed as the need to do so becomes apparent. Such screening is difficult but until this is done, widespread suspicions of 'risk' will inevitably persist (GILLESPIE & NEW 1998). Risk assessment for classical biological control is difficult, not least because an exotic species continues to evolve and adapt in its new environment, and may change its host or prey spectrum and tolerances to a wide range of environmental factors, but is a universal need in such cases. SIMBERLOFF & STILING (1996) emphasised that specific biological control projects should not be assumed to be innocuous until substantial effort has been made to support this assumption. Research and responsible regulation play important roles in this complex arena, with the primary responsibility of minimising collateral damage from introduced organisms. Wide consultation is occurring with increasing frequency, as is debate over quarantine issues associated with introduced agents (COULSON et al. 1991). Despite calls for 'group screening' procedures and exemptions for additional members of previously tested taxa, there seems little sound alternative to a species-by-species evaluation of risk.

Properties of desirable predators for biological control

An ideal insect predator for biological control of a given insect pest should be (1) specific or near-specific to that pest for prey; (2) respond rapidly in numbers to that prey when it is encountered, and should be voracious (VAN EMDEN 1966, included parameters of high appetite, high level of activity and high abundance: efficient killing and a high rate of capture success are implicit); (3) be able to detect the prey in low densities and track it effectively in the environment, whilst not dispersing to colonise neighbouring ecosystems; (4) be climatically adapted to the full (or near complete) geographical range of the prey, and naturally synchronised in time and space with the prey; (5) not be unduly disrupted by other environmental cues from efficient discovery and exploitation of the prey; (6) be tolerant/resistant to pesticides employed in the same IPM programmes, and (7) be generally compatible with other natural enemies for potential combined use. In addition, practical aspects such as amenability to economical mass rearing, perhaps using artificial diets, and inundative and augmentative release without undue dispersal from the release site become important in enhancing and manipulating the agent for greater efficiency.

Few, if any, species fulfil the above desiderata absolutely, and the science and credibility of biological control devolves on selecting the most suitable agents from a variety of suboptimal taxa available. Indeed, in many situations some of the above 'ideals' may not be so; for example, lack of extreme prey specificity confers practical advantages such as use of the same species against a variety of pest species, and allows use of other foods for subsistence during periods when the preferred prey is scarce or absent, thus providing for effective reservoir populations of the predator to be maintained between growing seasons of the target

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crop. Polyphagous predators may be of far more practical use than narrowly specific ones. Thus, PREE et al. (1989) advocated the use of C. *carnea* on the basis of its wide host plant and prey ranges. In Australia, *Mallada signatus* is promoted as a predator of aphids, mites, whitefly and Lepidoptera (HORNE et al. 1999). As with chemical pesticides, strict specificity can restrict marketing opportunity and, in view of the relatively high costs of mass rearing predators, a variety of target pests and crops is valuable to diversify the application of the species. However, in some cases polyphagous predators may eat other natural enemies and thereby interfere with other aspects of IPM. PRINCIPI & CANARD (1984) cited larvae of C. *carnea* eating nitidulid and coccinellid predators of date palm scale (*Parlatoria blanchardi*) in palm groves. Larvae may also eat aphids containing parasitoid mummies (TREMBLAY 1980). Cannibalism can also be problematical, with virtually all polyphagous species likely to eat conspecifics, and cannibalism likely to increase when other prey is scarce (DUELLI 1981).

C. *carnea* larvae can develop to maturity on a diet of conspecific eggs, and this was viewed by BAR & GERLING (1985) as a means to facilitate survival when other prey is scarce. Thus, under some circumstances, cannibalism can be adaptive (CANARD & DUELLI 1984). Sibling cannibalism is one (indirect) means to convert maternal tissue into offspring tissue. Instead of producing a few large eggs, a female lacewing can produce many small eggs, and cannibalism result in a few well-fed larvae. In conditions where larval food is abundant, many more may survive. Ability to colonise new areas might be advantageous in tracking a low density, dispersed pest. Problems and potential conflicts in IPM can thus arise when the same characteristics which render an introduced predator a useful, adaptable biological control agent essentially coincide with those which would render a species a dangerous invasive exotic from other points-of-view.

Many of the features of a given predator can be elucidated only by detailed study of the species, and only very limited generalisation should be made by extrapolation from data on other species, from species to higher category, and even from the same species on one crop to another crop or different environment. However, it is important to distinguish between an introduced predator species (for which specificity may be needed for effectiveness and to avoid undesirable side effects) and exploiting native predators occurring naturally in the area of operation and which may be polyphagous as part of the local community of indigenous consumers available for manipulation for IPM.

The criteria deemed important may depend also on the context for control. The prime aim of many biological control projects on crops is for short term control during the life of that crop, with the whole operation during this period of a few months or less, and repeated in its entirety the next season. The prime needs may then be for the predator to be an effective coloniser and build up numbers rapidly (LUFF 1983). Alternatively, biological control may be viewed as more permanent, with the establishment of agents providing long term benefit.

A functional difference between these approaches is often that introduction of a classical biological control agent is expected to regulate its target prey by density-dependent action, and should therefore be specific, whereas augmentation of naturally occurring predators is viewed as a short term measure. The latter is therefore not usually intended to maintain the pest below economic threshold levels, but as a 'therapeutic' control of temporarily high prey numbers (NORDLUND 1996). Specificity is therefore not required for predation to be an effective method of suppression in the field.

Most use of lacewings is indeed in such augmentative releases, involving aspects of mass production and repeated releases with potential for genetic alteration or various forms of behavioural modification using semiochemicals. Species such as C. *carnea* are well adapted to short duration habitats, such as annual cropping systems. Annual crops are frequently highly disturbed habitats, monocultures which are very unstable, and with inadequate natural chemical defences against pest attack. The biological variability within the '*carnea* complex' may allow for selection of appropriate forms suitable for different crops

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and regions. In annual crops, augmentative releases of natural enemies are viewed increasingly as 'inundative' to cause immediate mortality, so that measurement of mortality is a critical aspect of monitoring success (OBRYCKI et al. 1997). Enhancing the effects of released predators through optimal release strategies and local environmental manipulation is an integral part of such exercises.

Lacewings as 'ideal predators'

Relatively few Neuroptera appear to be specific in their choice of prey species, but opportunistically take a variety of prey taxa (NEW 1986). Limitations may be more on the grounds of physical compatability and ease of capture, rather than on strict taxonomic grounds. Thus, lacewings are only rarely reported as predators of Thysanoptera in Europe (RIUDAVETS 1995), probably because thrips are 'tough'. However, CHANG (1998) reported larvae of *C. plorabunda* (FITCH) to consume more thrips than aphids and suggested that they might have value in controlling them in some field crops in North America. Most prey reported commonly are relatively soft-bodied taxa, such as aphids, other Homoptera, mites or small caterpillars, with some lacewings apparently associated reasonably consistently with one or more of the above groups, which collectively contain a high proportion of herbivorous crop pests. Relatively few complete surveys of the prey spectrum of lacewing species have been made, and the relationships between habitat specificity and food specificity are commonly not clear. For example, species of Coniopterygidae or Hemerobiidae associated consistently with either coniferous or broadleaved trees in the northern hemisphere (MONSERRAT & MARIN 1996) are clearly restricted to developing on prey species on those tree groups and thus correspondingly limited in distribution. But whether habitat restriction mediates prey restriction or the converse is not easy to determine. In some other cases, sporadic records of prey association have been translated into broader dogma without critical reappraisal.

Most lacewing taxa implicated as useful predators are simply those which have been studied, or which have been found with the pest species of concern. Their practical values are based commonly on flimsy evidence, mainly co-incidence and the undoubted voracity of many lacewing larvae. Numerous early records (summarised by NEW 1975) show that individual larvae of all three families may consume up to several hundred prey individuals as they develop. Many such records include impressively high numbers, but most do not differentiate between 'prey killed' and 'prey eaten'; partial consumption of prey is frequent among insect predators (NEW 1991), and many of the problems of interpreting voracity are noted by PRINCIPI & CANARD (1984). From the practical viewpoint of reducing pest numbers, of course, 'killing without eating' is a perfectly satisfactory outcome! NEUMARK (1952) reported two larvae of *Chrysoperla carnea* as devouring 6487 and 4645 eggs of *Matsucoccus*, respectively. *C. plorabunda* and several related species in California can eat more than 200 cotton aphids (BURKE & MARTIN 1956). Larvae of smaller hemerobiids and coniopterygids are similarly voracious. Data for Coniopterygidae, summarised by LO VERDE & MONSERRAT (1997), clearly imply the likely value of some species as control agents but, again, much of the information on this family needs corroboration and further research. They are generally deemed likely to be important in biological control of insect pests (TAUBER & ADAMS 1990), but are 'usually overlooked because of their small size' (PENNY et al. 1997).

Attributes of both larva and adult stages are relevant in evaluating the likely impacts of lacewings on prey populations. Whereas both stages are predators in Coniopterygidae, most Hemerobiidae and some Chrysopidae, adults of some Chrysopidae (including many of those predominantly valued in pest control) feed on honeydew or nectar, thus requiring different food sources from their larvae.

There have been relatively few comparative trials on the suitability of particular prey species to particular lacewing species, with their influences on development, fecundity and general fitness reported. CANARD's (1970, 1972) classic study of the suitability of five aphid species as prey for *Chrysopa perla* larvae indicated some important effects on adult biology. Thus, although *Megoura viciae* supported larval development and was readily eaten,

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resulting adults had very low fecundity, with males sterile. Many such effects were summarised by PRINCIPI & CANARD (1984), showing influences of food on duration and extent of chrysopid development, differential mortality, and adult performance. Some prey can be toxic, even though they are acceptable to lacewing larvae. The main conclusion is that studies of food utilisation and acceptability may need very careful conduct as 'information published on the feeding habits of Chrysopidae in nature is often imprecise' (PRINCIPI & CANARD 1984).

Two Australian Hemerobiidae compared by NEW (1984) differed considerably in their relative response to Psyllidae and cabbage aphids (*Brevicoryne brassicae*) as prey. The generalist *Micromus tasmaniae* WALKER performed well on both prey species, but the more specialised arboreal *Drepanacra binocula* (NEWMAN) appeared to be much the better adapted to native psyllid prey. However, laboratory trials of the sort reflected in such studies may not always adequately represent the field situation in which a variety of prey species may coexist, and may overlook some other aspects of the interaction (FRAZER & GILBERT 1976). In general, 'specialist' predators may be expected to be adapted in various ways to their prey of choice whereas generalist species may show less distinct differences on different prey species. Many of the lacewings used commonly in biological control fall into the latter category.

Prey specificity can be based on a broad variety of genetically controlled traits (TAUBER & TAUBER 1987), including (a) choice of oviposition site, (b) adult food requirements for mating, (c) large egg size, (d) specialisations of larval behaviour, (e) enhanced larval development and (f) univoltinism. TAUBER & TAUBER showed that considerable genetic variation underlies the feeding differences between the monophagous *Chrysopa slossonae* (which feeds only on a single aphid species, *Prociphilus tesselatus* (FITCH)) and the generalist C. *quadripunctata*. Young larvae of C. *quadripunctata* suffered high mortality in presence of this aphid (ALBUQUERQUE et al. 1997), and clear species-specific defensive and feeding behaviour patterns occur in these two sister-species (MILBRAITH et al. 1993)

However, polyphagy is a complex state to appraise. It can enable a predator to extend and diversify its habitats and ecological influences. Food quality, though, can vary greatly not only between prey species (so that some prey are 'essential food' for particular predator species in that they are adequate to support reproduction, whereas others are 'alternative food' which support development but not reproduction), but also within a prey species, depending on its own nutritional regime. Influence of suitability of a particular prey species to a predator can vary seasonally. In a broad appraisal of predators' diets in arable ecosystems, SUNDERLAND et al. (1996) suggested that 'It seems likely that, in general, more than one prey type is needed by predators to maximise fitness'. Polyphagy allows for augmentation of limited supplies of high quality foods to ensure adequate energy and nutrients to grow, develop and reproduce.

Searching behaviour by lacewing larvae is efficient, with details of search pattern changing once prey is encountered during extensive wandering, to more intensive patterns.

The complexity of the plant substrate may 'guide' how predators search in particular environments. Plant structure may also affect the susceptibility of prey, by providing refuges in which they can hide. C. *carnea* larvae are more effective in reducing populations of Russian wheat aphid (*Diuraphis noxia* (MORDVILKO)) on Indian rye-grass (*Oryzopsis hymenoides*) than on crested wheat grass (*Agropyron desertorum*), and MESSINA et al. (1995, 1997) attributed this in part to the narrower blades of the former, so that lacewings could then rarely pass an aphid without contacting it. Their capture rate was therefore higher, but also led to many aphids contacted falling from the plant. On crested wheat grass, fewer aphids were contacted and fewer were dislodged, so contacts were more likely to result in capture (CLARK & MESSINA 1998).

Diet substantially influences egg production by lacewings, and the size of eggs in particular species may be related to prey specificity (TAUBER & TAUBER 1987). Fecundity of all three families is usually in the order of hundreds, and can extend much higher in some species. With rapid growth rates in the warmer parts of the year, some species can respond

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rapidly to abundance of suitable prey. Adult diet is also highly influential, with dramatic responses found in two species of *Chrysoperla* by CARVALHO et al. (1996). Females fed on high quality diet (yeast plus honey, 1:1) laid an average of 2304 ± 188 eggs (C. *externa*, n = 6, oviposition period 84.5 ± 10.5 days) and 2160 ± 159 eggs (C. *mediterranea*, n = 6, oviposition period 103.3 ± 8.6 days). The poorest food tested, pure honey, in contrast led to outputs of only 25 ± 6 and 94 ± 20 eggs, respectively for the two species. Measures of reproductive performance in lacewings must be related clearly to both larval prey suitability and adult diet. Protein and carbohydrate are both needed by adults of such species for good reproduction, but measuring the efficiency of food utilisation is difficult.

Single or multiple predator species?

The question of whether to use single species of natural enemy in a given pest control operation, or a combination of species, remains controversial, with one key argument being whether different predators may interact in an 'additive way' (CHANG 1996) to enhance control, or interfere with each other to reduce overall control success. Such influences for generalist predators may include interspecific cannibalism. Support for both viewpoints exists, and there is probably no universal answer in view of the great variety of predatory insects and strategies (NEW 1991). Some cases of complementarity may be reasonably clearcut: in field crops in southeastern Australia a single common hemerobiid (*Micromus tasmaniae*) is mainly aphidophagous and a manipulable chrysopid (*Mallada signatus*) feeds easily on lepidopterous larvae, prey not favoured by *Micromus*. The two species may thereby complement each other for multi-pest contexts.

CHANG (1996) undertook laboratory trials to determine the larval behaviour of C. *plorabunda* and the ladybird *Coccinella septempunctata* whilst feeding on bean aphids (*Aphis fabae* SCOPOLI), but found no clear evidence of interactions between these species, probably reflecting that the larvae tend to occur in different places on the plant so that they rarely encountered each other.

Increased compatibility between different predator species may be achieved if they interact in ways which serve to reduce the likelihood of competitive effects between them, and increase their collective influences on a prey species. Some chrysopid larvae have been shown to secrete an oviposition-deterring pheromone (ODP), which deters females from laying eggs at sites searched previously by larvae. The effects of this can extend beyond intraspecific influences, to interactions of different species and genera, so that the chrysopid ODPs are also allomones (RUZICKA 1997a, b 1998, RUZICKA & HAVELKA 1998). Substrates contaminated by chrysopid ODP deterred a ladybird, C. *septempunctata*, from laying.

The ODP of C. *oculata* SAY persists for several weeks and is relatively stable up to about 140° C. Unfed first instars, as well as later stages, mark the sites they search for prey (RUZICKA 1994). The ramifications of this behaviour are complex and remain to be investigated in detail. Predators may, for example, be able to avoid others which would eat them if prey were scarce, so that there may be advantage in spreading offspring more evenly between patches of aphids. This would be achieved by females searching for ODP-free sites. In practical terms, this might lead to a higher efficiency of aphid control. Conversely, as RUZICKA & HAVELKA (1998) noted, a strong female response to ODPs (or ODAs) might favour growth of aphid colonies which survive the 'first wave' of predators but are still protected by those deterrents for some time.

Females of C. *perla*, C. *commata* and C. *carnea* tested by RUZICKA (1998) all strongly avoided oviposition on substrates contaminated by their own larvae or the other species in this group.

Nevertheless, intraguild predation may be responsible for low numbers of lacewings found after some commercial releases (ROSENHEIM et al. 1993). Intraguild predation is very common (POLIS et al. 1989). The egg-stalks of chrysopids have commonly been presumed to confer protection from other predators, but the eggs are indeed vulnerable to ladybirds (LUCAS 1998) and others. The effects of predators may vary also depending on whether one or several species of prey are present. Presence of alternative prey may simply provide a

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distraction, especially if it is more easily accessible than the target species. Conversely, the presence of one herbivore species can increase the susceptibility of a second species - for example by presenting a resource attractive to predators and increasing their abundance and feeding intensity in a habitat patch. Trials on the interaction between the bird cherry-oat aphid (*Rhopalosiphum padi* (L.)) and the Russian wheat aphid (*Diuraphis noxia*) suggested that C. *plorabunda* can control the latter on range grasses, but its effectiveness may be hampered by presence of such other cereal aphids. Presence of *R. padi* may have reduced predation on *D. noxia* because *R. padi* is the more accessible species or because its faster growth rate caused it to outnumber the other species on plants that initially received equal ratio of the two species (BERGESON & MESSINA 1997).

Integrated pest management

Integration of natural enemies with insecticide use and other methods of suppression is a priority in developing integrated pest management, so that themes such as insecticide tolerance and resistance become central to development of practical programmes. A wide variety of pesticides used in agriculture also affect beneficial insects, and knowledge of these effects is clearly important in designing pest management regimes. Early studies of integration of chrysopids with pesticide use were reviewed by BIGLER (1984), who noted the apparent advantages of Chrysopidae for IPM as reflected in their physiological and ecological tolerances to a variety of pesticides then widely used.

a. Chemical pesticides.

The effects of pesticides on arthropod natural enemies of agricultural pests have been reviewed extensively (THEILING & CROFT 1988, HOY 1990), but some lacewings had earlier attracted attention because of their apparently natural tolerances, based on laboratory trials with larvae. Some generalities thereby started to emerge - such as the likelihood that Chrysopidae are more tolerant than Hemerobiidae to pyrethroid insecticides (CROFT 1990). C. *carnea* has figured highly in such trials, as one of the insects most frequently tested for insecticidal effects (CROFT 1990); indeed, it has been adopted as a 'representative predator' in such studies, simply because of the extent of background knowledge and the easy availability of the lacewing for trials. GRAFTON-CARDWELL & HOY (1985a) enumerated laboratory trials on 128 different pesticides. Many of these were difficult to evaluate because of the different methods and protocols used, and differences in the stages or age classes tested. However, all stages were highly tolerant of many of the pesticides evaluated. High susceptibility to field dosage rates of most carbamates and organophosphorous insecticides prompted a survey of interspecific variability, as a prelude to investigating development of resistance in the laboratory.

Other extensive trials on C. *carnea* from Californian alfalfa fields were summarised by HOY (1990). Eggs, larvae and adults from four colonies were screened with six pesticides (carbarylmethoxyl [carbamates], permethrin, fenvalerate [pyrethroids], diazinon, phosmet [organophosphates]). Populations from the four locations responded with significant differences to all six chemicals; one population consistently had highest mortality, one the lowest, and the other two were intermediate. Differences in survival corresponded generally with pesticide usage in the alfalfa. This survey was important in suggesting that populations of C. *carnea* responded to local pesticide selection pressures, and implied that geographical differences in tolerance reflect past selection pressures (PREE et al. 1989).

HOY (1990) summarised detailed earlier studies (GRAFTON-CARDWELL & HOY 1985a, 1985b, 1986) in which this intraspecific variability and trials for selection for insecticide resistance were discussed in more detail. Selection response with carbaryl led to a rapid and high level of resistance; the resistant strain could not be killed after the third selection by a wide range of concentrations of the pesticides, and the resistance may be determined by one or few major genes (GRAFTON-CARDWELL & HOY 1986). Changes in fitness due to laboratory rearing were compared between the 'base' and 'resistant' colonies, to determine any differences in performance. Larvae and pupae of the base colony had higher survival rates than the resistant strain, but

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duration of development did not differ significantly between the two colonies. The fecundity of resistant females was slightly the higher, but percentage hatch of eggs did not differ. Methods for screening the various stages were developed by these authors.

In addition to intraspecific variations and changes in tolerance to pesticides, tolerance may differ greatly between species (ROUSCH 1995) but, as ROUSCH noted, this does not usually influence biological control in practice because primary choice of agents is mainly by other criteria. In contrast, pesticide resistance is of greater relevance because it implies greater variation which allows some individuals to tolerate doses which are normally lethal.

Assumptions that particular pesticides or groups of pesticides are 'safe' for use in conjunction with particular groups of natural enemies are based commonly simply on the lack of conspicuous lethal effects. However, a wide variety of sublethal effects, many of them difficult to enumerate and evaluate, may also cast doubt on the values of some such chemicals. For example, insect growth regulators (IGRs) have been presumed generally to be compatible with IPM, and have been defended as such (HATTINGH 1996), from the reasoning that since they interfere with specific metabolic pathways of pests they are more selective to natural enemies than conventional insecticides (CROFT 1990). They often interfere with natural enemy development and their biological control capacity. Following documentation that IGRs can have severe detrimental effects on populations of some beneficial coccinellids, RUMPF et al. (1998) showed that they can have more severe effects on *Micromus tasmaniae* than organophosphorous insecticides and a pyrethroid they tested. Effects of three IGRs (fenoxycarb, diflubenzuron, tebufenozide) were compared with those of two organophosphates (methyl parathion, azinphos-methyl) and a pyrethroid (permethrin) for life table parameters determined for adults reared from treated larvae and controls. The effects noted included (1) a higher proportion of female lacewings (diflubenzuron), (2) reduced longevity (fenoxycarb, diflubenzuron), (3) total number of eggs redued for one generation (fenoxycarb, diflubenzuron) and the following generation (tebufenozide), and (4) daily oviposition rate reduced (diflubenzuron).

Literature on the sublethal effects of pesticides continues to expand. The IGRs noted above represent the recent trend toward using more slowly acting pesticides with a more selective mode of action. They differ in their precise modes of action: fenoxycarb is a juvenile hormone analogue, diflubenzuron is a chitin synthesis inhibitor, and tebufenozide is an ecdysone based moulting inducer. This variety suggests the likelihood that IGRs will be found to have a substantial array of undesirable effects on natural enemies, and clarifying these is urgent in helping dispel the illusion of safety such chemicals have fostered. HATTINGH & TATE's (1995) studies in South Africa demonstrated clearly that IGRs can interfere with biological control by coccinellids. A second chitin synthesis inhibitor, triflumuron, applied topically to adult *C. carnea* did not affect fecundity or longevity at doses tested by SENIOR et al. (1998), but egg and larval development were both substantially retarded. First instars were the most heavily affected. An effective dose can be obtained by larvae simply by tarsal contact (SHUJA et al. 1998). Severe effects, with mortality of up to 100 %, of chitin synthesis inhibitors on *C. carnea* were noted also by BIGLER & WALDBURGER (1994), although earlier studies by WILKINSON et al. (1978) had shown no effects on adults or larvae, but substantial pupal mortality. VOGT (1994) also found substantial effects on larvae and pupae of this species.

Case by case evaluation is needed to assess effects of IGRs, as for any other group of pesticides. Sensitive measures of sublethal exposures to insecticides, such as toxin-specific rate of head acetylcholinesterase (AChE) inhibition, may be of some value in studies of impacts of particular chemicals on lacewings. Activity of AChE was inhibited much more rapidly in *M. tasmaniae* than in *C. carnea* larvae, corresponding to higher tolerance of the latter in mortality tests (RUMPF et al. 1997), and again confirming the dangers of trying to generalise about insecticide effects on larger taxonomic groups.

b. Biological pesticides.

Protocols for testing for side effects of

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microbial pest control agents have been developed mainly because of use of specially engineered pesticides, such as forms of *Bacillus thuringiensis*. CROFT (1990) used C. *carnea* as a representative model predator to discuss formulation of standard protocols for evaluation. For adults, ingestion and direct contact, because of direct penetration of the integument (by fungi) was recommended for tests, whereas the wider activities of larvae suggested need for three categories of tests: (a) topical, with larvae (with introduced prey) tested in cages which have been sprayed with the pesticide and allowed to dry to leave residue; (b) feeding larvae on prey sprayed with the pesticide, and (c) feeding larvae on prey which have ingested the pesticide. For the last two trials, feeding for seven day periods was recommended.

The entomophagous fungus *Verticillium lecanii* has been used successfully as a microbial insecticide against aphids in greenhouses, and has recently been tested for effects on C. *carnea* as an important predator in the same environments. Larvae of C. *carnea* were treated with the fungus by immersion, and fungus-treated aphids (A. *craccivora*) were fed to third instar larvae. Feeding capacity of larvae was decreased by both treatments. Likewise, both direct infection and feeding on fungus-infested aphids increased duration of the larval and pupal stages; and feeding on infected aphids reduced the proportion of adults that emerged, due to contamination within the cocoon. Searching capacity of larvae was also impaired by infection (SEWIFY & EL ARNAOUTY 1998).

Under laboratory conditions, larvae of the closely related C. *kolthoffi* were highly susceptible to *Metarhizium anisopliae*, the green muscardine fungus, one of the most widely used fungi in microbial control (VENTURA et al. 1996).

Commercial *Bacillus thuringiensis* (Bt) insecticides have been used predominantly against lepidopterous pests, and transgenic crop plants incorporating endotoxins from the bacterium are now being introduced. The safety of genetically engineered crop plants of this nature is currently of considerable concern. Prey fed with Bt may cause death of predators. Trials with C. *carnea* by HILBECK et al. (1998) revealed much higher mortality in larvae reared on Bt-fed lepidopterous larvae (62 %) compared with Bt-free prey (37 %). 'Sick' prey may also cause nutritional deficiencies in predators, but HILBECK et al.'s study suggested that reduced fitness of C. *carnea* was indeed associated with Bt. More limited trials by SALAMA et al. (1982) had earlier suggested that C. *carnea* larvae had prolonged development and reduced food intake when fed on *Spodoptera* larvae fed on a diet containing Bt, but those larvae were fed the test diet for only seven days, and then returned to normal, healthy prey.

Tests of the effects of nuclear polyhedrosis virus from a noctuid moth on larvae of C. *carnea* (HASSAN & GRONER 1977) revealed no influences on larvae, or on fecundity of resulting adults (or viability of their eggs) when larvae were sprayed directly, fed on infected diet, or exposed to residual film of the sprays.

c. Cultural controls.

Considerations of larval and adult behaviour of lacewings can affect their use in conjunction with 'cultural controls' such as intercropping, and changing tillage regimes in crops to help conserve natural diversity. Counts of chrysopid eggs (species, singular or plural, not specified or separated) on cotton in Nicaragua interplanted with corn, beans or weeds (SCHULTZ 1988) revealed some significant numerical differences. Significantly fewer eggs were found on cotton interplanted with corn or weeds than in monocultures. In this case, crop diversification was apparently associated with reduced numbers of beneficial insects, contrary to the results of many other, similar appraisals, and corroboration of this would be of considerable general interest.

Manipulating lacewings for biological control

The foregoing has confirmed that lacewings, at least of a few generalist taxa, can play very positive roles in a variety of pest control contexts, but predominantly for short-term manipulation to control seasonal pests on field and glasshouse crops. The biological basis of their values is reasonably well under-

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stood, and underpins also the ways in which the lacewings can be manipulated for enhanced value in integrated pest management. Use of C. *carnea* and its close allies, in particular, has led to development of commercial mass-rearing operations in North America and Europe, which have spawned similar operations elsewhere for other species of potential value. Much of this draws directly on the pioneer work by HAGEN and his colleagues in California, by which the use of artificial diets, and of attractant principles for field manipulation were established as a solid basis for later development and refinement.

However, some taxonomic confusion is still apparent in the precise species used. In a recent survey, O'NEILL et al. (1998) reared insects sold in the USA by three commercial insectaries as C. *carnea*; although their sample was small, all individuals reared were C. *rufilabris*, a species not usually placed in the *carnea* complex. Although C. *rufilabris* is indeed supplied extensively by commercial insectaries in the United States (HUNTER 1997), its biology differs considerably from that of C. *carnea*. As noted earlier, such confusions can have far-reachng consequences in evaluation of control success, and in broader conservation issues. As with most aspects of mass-rearing of natural enemies, adequate quality control is vital. Additional point-of-sale evaluations by O'NEILL and his colleagues showed the importance of posting at a correct, critical stage of development. Chrysopids are posted as eggs in most operations, usually with a supply of food (such as *Sitotroga* eggs) to sustain larvae as they hatch, but hatching of larvae en route can lead to considerable cannibalism. The percentage alive on receipt was generally in the range of 60-80 %, but addition of supplementary food is clearly advantageous, and rapid release of the agents may also be necessary to avoid further deaths from starvation or cannibalism in confined surroundings. Most such releases are to open field systems (DAANE et al. 1997), notwithstanding the values also of lacewings in glasshouses (SCOPES 1969), where both C. *carnea* and wholly predatory species (such as *Chrysopa perla*) may be useful.

The precise method of release can also have far-reaching consequences. Three aspects of this (the developmental stage released, the mode of delivery and the release rate and timing) were evaluated in California vineyards in trials against leafhopper pests (DAANE & YOKOTA 1997). Chrysopids are usually released as eggs, with the caveats of losses from cannibalism during shipment and any period of delay before deployment, but DAANE & YOKOTA noted the possible advantages of larval release because the voracious third instar stage would be reached more quickly, and predatory pressure increased rapidly in the field. This might also help to reduce intraguild predation in some circumstances. In Californian cotton fields, the dominant predatory arthropods other than lacewings are Heteroptera. Suspicion of predation by the bugs on lacewing eggs was raised by the great differences in field abundances of chrysopid eggs (common) and larvae (rare). ROSENHEIM et al. (1993) believed that decreased survival of lacewing larvae was primarily due to predation by Heteroptera. It occurred despite prey being abundant.

However, releases of eggs by DAANE & YOKOTA (1997) gave very low hatchability (28.4 ± 12 % of eggs), and this high mortality was attributed tentatively to high temperatures in the vineyards, coupled with a relatively long pre-hatching period because freshly laid eggs were used. Point-of-hatch eggs may be a more suitable release stage in increasing survival, despite prior risks of cannibalism from 'early hatchers'. Release of eggs gave no differences in leafhopper numbers when compared to untreated control plots, but significant reductions occurred from larval releases and high survival of third instars.

Various systems have been developed for releasing lacewings in the field. Those tested by DAANE & YOKOTA (1997) ranged from 6 175 to 1 235 000 eggs or larvae/hectare, but showed no correlation between numbers released and prey density.

The production and manipulation of chrysopids, in particular, for augmentative control has achieved a high level of success. The stages of a commercial operation are (1) mass rearing, with use of artificial or semiartificial diets for larvae and adults, (2) holding adults and harvesting the eggs for sale and colony maintenance, (3) optimising releases and (4) monitoring and maintaining the

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released populations in the vicinity of the crop. Early developments in this field were described by TULISALO (1984). Some hemerobiids also show considerable promise for this approach, with mass rearing for *Micromus angulatus* in Europe described by STELZL & HASSAN (1992).

Mass rearing must be cost effective, and considerable efforts continue to refine the process, depending increasingly on artificial diets and progressive automation of the production process. Again, most work has been undertaken on species of *Chrysoperla*. NORDLUND & MORRISON (1992) identified major areas for attention as larval food composition and presentation, adult feeding and oviposition effects, mechanised egg collection and de-stalking, mechanised larval rearing units, preceding field application. Details of all these stages are readily available, but the main biological interest is in understanding and exploiting the insects' feeding habits and patterns of development and movement in relation to producing large numbers efficiently and enhancing their effects in the field.

The use of artificial diets for lacewings is by no means new, extending back some 50 years, with HAGEN's (1950) studies of protein requirements in adult diet still of fundamental importance. These early diets were liquid-based, but recent trends to develop more solid diets for chrysopids, to better resemble the texture of their normal prey (COHEN 1998, COHEN & SMITH 1998) appear likely to improve both quality and quantity of the insects produced. However, even simple 'artificial honeydew' (commonly a mixture of sucrose, yeast and water) can facilitate larval development and be of practical importance in allowing C. *carnea* to develop at low prey densities.

Adult diets for such glyciphagous species have incorporated yeast hydrolysates and sugars to produce high reproductive activity and, again, those diets derived from HAGEN's work (for example, HAGEN & TASSAN 1966) to enhance protein content have been used frequently since that time. However, particular constituents of adult diet may be critical in affecting fecundity (MCEWEN et al. 1995), and in field manipulation through their attractant properties. Food sprays have been employed to concentrate lacewings in particular areas of crops, with sprays of artificial honeydew containing acid hydrolysed L-tryptophan effective in increasing numbers of C. *carnea* (HAGEN et al. 1976, VAN EMDEN & HAGEN 1976). Refinement of this approach is continuing (MCEWEN et al. 1994),

Capitalising on lacewing lifecycles in biological control necessitates understanding of any diapause regime and the factors which control seasonal development. This is also relevant in designing optimal regimes for storage of reared material without loss of reproductive performance and general viability. TAUBER et al. (1993) showed that C. *carnea* adults can be maintained at low temperatures for around six months without significant reduction in fertility or fecundity. CHANG et al. (1995) extended that study to show that storage under short day (8 hour light: 16 hour dark) conditions at 5°C , with a carbohydrate and protein diet, gave post-storage adults whose reproductive performance equaled that of 'normal' unstored adults. The implications of this were seen as reducing investment in facilities and labour without loss of product quality. CHANG et al. proposed a protocol which could be tailored both for short-term and long-term maintenance of the lacewing. Considerable variation in the life history traits of this species suggested the need for different storage strategies for different populations (TAUBER et al. 1997b).

C. *externa*, some populations of which do not diapause, is restricted to relatively warm conditions, but trials on storage at 10 ° C showed considerable possibility for keeping stocks for release (TAUBER et al. 1997a). Adults survived well for at least four months, though oviposition rates declined from two to four months in storage.

Dispersal of liberated predators from the release site can obviate any desirable longer term benefit. As DUELLI (1980) showed, C. *carnea* undertakes migratory flights soon after emergence and may thus leave the areas where it is needed. Use of semiochemicals, as above, is important in helping to maintain populations in crop environments, but MCEWEN et al. (1998) also described the use of overwintering chambers for adult C. *carnea* to help stabilise populations. These chambers provide

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adults with a focal retreat, by which overwintering survival could be enhanced considerably; the chambers may also be transportable to provide inocula of adults for fresh sites in spring.

The extensive work summarised above for C. *carnea* and its relatives is among the most wide-ranging and informative bodies of data on any insect predator, and displays the varied uses for generalist predators in biological control. As PARRELLA et al. (1992) emphasised, such use of native natural enemies is likely to become increasingly important in IPM, and marks a determined transition from the importation of specialist natural enemies and classical biological control. Use of specialist predators is likely to continue in control of particular pests, but the effective integration of C. *carnea* (s.l.) with a variety of other facets of IPM renders it exceptional. Further studies of the complex, and of other chrysopids will undoubtedly extend their range of applications.

A number of generalist hemerobiids clearly also merit additional attention for enhancement and manipulation in crops. The tolerance of some hemerobiids to lower temperatures than many chrysopids can withstand can render them useful for control purposes at times when chrysopids are not active. Thus, species of *Hemerobius* in California are active throughout the year and *H. pacificus* is the only common active predator in artichoke fields during the winter (NEUENSCHWANDER 1975, NEUENSCHWANDER et al. 1975, NEUENSCHWANDER & HAGEN 1980; further details in NEW 1988) and its use might extend the overall period of effective control by lacewings. M. *tasmaniae* in Australia and New Zealand might play a similar role, and other parallels may be sought in other places.

There would appear to be considerable potential to manipulate other species of lacewings to increase their values as inoculative control agents in a broad variety of pest control contexts, and to improve the selection of species for use in a wide variety of habitats and climate regimes.

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Zusammenfassung

Bisher sind Arten von drei Familien der Neuroptera – Coniopterygidae, Hemerobiidae und Chrysopidae – in der biologischen Schädlingsbekämpfung bzw. im integrierten Pflanzenschutz eingesetzt worden, vorwiegend zur Bekämpfung von Schädlingen von Feldfrüchten und im Rahmen von Programmen zur Steigerung der Einbindung natürlicher Feinde. Besondere Aufmerksamkeit wurde einigen Chrysopiden, vorwiegend Arten der Gattung Chrysoperla, geschenkt. Die gegenwärtigen Entwicklungen werden umrissen, und Möglichkeiten für einen vermehrten Einsatz von Neuropteren in der Zukunft werden diskutiert.

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